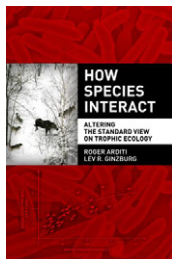


# The case for ratio dependence in trophic ecology

**How Species Interact: Altering the Standard View on Trophic Ecology** by Roger Arditi and Lev R. Ginzburg. Oxford University Press, 2012. 204 pp. \$59.00/£40. ISBN 978-0-19-991383-1

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It can be argued that predation is the fundamental process of ecology. It follows that ecologists must understand how the predation rate depends on the populations involved, of both predator and prey, to understand the behavior of food webs. The theme of this book is that this dependence has been largely misunderstood, with consequences for ecological theory and its applications. In particular, in most

current predator–prey and food web models, the per capita predation rate, or predator functional response, is assumed to be a function of prey density alone, and is thus termed prey-dependent (PD). The authors argue that more basically, the dependence of the functional response should be on the ratio of prey density to predator density. Versions of the ratio-dependent (RD) response, as the authors coin it, have been around for a long time but did not arouse controversy until the authors published a paper on their own Arditi–Ginzburg (AG) ratio-dependent functional response model [1]. The authors explored the consequences of the AG functional response for predator–prey and food web dynamics, and found that many of the consequences are very different from classic predator–prey theory based on PD responses, such as the well-known Holling type 2. A number of ecologists were quick to argue that, among other things, the AG and other RD models are not based on a formal mathematical derivation, unlike PD models, which are derived mathematically by imagining following an individual predator's instantaneous search for and capture of prey items. These and other criticisms have since been met with cogent responses and RD models are now accepted sufficiently to be included in major textbooks on ecological theory. Nonetheless, PD responses remain far more common than RD in theoretical papers.

In this compact book the authors marshal a set of arguments to support their view that RD, rather than PD, should be the central model for predator–prey interactions. After noting that an RD functional response model [2] has been used successfully in microbiology for many years, the authors describe analyses of ecological data from laboratory and field studies, comparing the ability of PD and RD models to fit the data. The analyses show that all functional responses calculated from the considered examples exhibit significant dependence on predator density, rather than prey density alone. In the following chapter the authors compare PD and RD using indirect evidence from the behavior of empirical food

chains. The PD response predicts that increasing primary productivity should lead to an increase in only alternating trophic levels, and should lead to greater instability of the chain (termed the paradox of enrichment). Both of these predictions have been hard to demonstrate outside of laboratory conditions. The authors argue that RD, by contrast, is consistent in both cases with empirical data. Although neither of these lines of evidence is proof of the RD model, they at least suggest a reassessment of PD as a starting point for either theory or applications.

The authors demonstrate that RD is an emergent property of ecosystems due to temporal variability in populations and spatial heterogeneity in their environment. Arditi and Ginzburg here take the offensive against what they call the instantists, who claim that a differential equation model of predators and prey must be based on following predator search and prey capture instantaneously in continuous time. As the authors note, however, no populations change in a purely continuous manner, and many have distinct breeding periods. This argues for following population change on a coarser time scale than that on which individuals interact. That is what RD does, by implicitly taking into account the way that predators affect each other's interactions on a coarser time scale. The authors also demonstrate that RD emerges when interactions are averaged over spatially heterogeneous environments that include prey refuges. Spatial behavioral phenomena such as clustering and directionality of movement are also shown to lead to RD responses. The authors finally highlight the sense of beauty and symmetry in the RD model. Unlike PD, RD allows for simultaneous exponential growth of both prey and predator under certain conditions. This property of ecological invariance makes intuitive sense, so RD should attract attention on that basis alone.

This book should nudge ecologists to give equal consideration to both PD and RD in developing predator–prey and food web models, from which ecology will benefit. Any reader who wants a thoughtful and deep consideration of the issue will be richly rewarded by this book.

## References

- 1 Arditi, R. and Ginzburg, L.R. (1989) Coupling in predator–prey dynamics: ratio dependence. *J. Theor. Biol.* 139, 311–326
- 2 Contois, D.E. (1959) Kinetics of bacterial growth: relationship between population density and specific growth rate of continuous cultures. *J. Gen. Microbiol.* 21, 40–50

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